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THE REPRODUCTIVE PHYSIOLOGY OF THE INTERTIDAL PROSOBRANCH *THAIS LAMELLOSA* (GMELIN). II. SEASONAL CHANGES IN BIOCHEMICAL COMPOSITION[1]

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Relatively few investigations have been published on seasonal changes in the biochemical composition of marine prosobranch gastropods. Blackmore (1969) followed seasonal changes in the level of polysaccharide, lipid, non-protein and protein nitrogen in the limpet *Patella vulgata*. Several papers have been published on seasonal changes in the biochemical level and content of the abalone *Haliotis cracherodii* (Giese, 1969; Webber and Giese, 1968; Webber, 1970). Williams (1970) followed seasonal changes of lipid and carbohydrate level in the periwinkle *Littorina littorea*. Lambert and Dehnel (1974) followed seasonal changes in the biochemical level of several body components and in the digestive gland and gonad indexes of *Thais lamellosa*. They also obtained histological data on feeding activity and gamete maturation.

This investigation deals with seasonal changes in the concentration (level) and absolute quantity (content) of protein, lipid, and polysaccharide in body components of adult *T. lamellosa*. The biochemical composition of its egg capsules and partitioning of female energy during aggregation are also determined. Seasonal changes in the size of the body components (indexes) and respiration rates of this population were previously reported (Stickle, 1973). Aggregation occurred after November 18, 1968 and was completed by March 27, 1969. Egg capsule deposition began between January 7 and 19, 1969 and was completed by March 27, 1969. The accessory reproductive tract of this species consists of an albumin gland and a capsule gland which deposit nourishment for the developing embryos. Lyons and Spight (1973) followed embryological development within the capsule and found snails to emerge from the capsule as crawling juveniles.

METHODS AND MATERIALS

Body components

Animals were collected from Turn Island, Washington and dissected into body components (Stickle, 1973). Male soft body components consisted of the visceral mass and its subdivisions (the testis-digestive gland complex and the remaining visceral mass) and the foot. Female soft body components consisted of the visceral mass and its subdivisions (the ovary-digestive gland complex, the capsule-albumin gland complex and the remaining visceral mass) and the foot.

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Samples from the November 1969 and January, February, and March 1970 collections were not analyzed because they thawed during shipment and were not considered suitable for chemical analyses.

Level and content

The level of each biochemical class is presented on a milligrams per gram dry weight basis. Nutrient content is calculated by multiplying the level times the body component index and expressing content in grams. The component index used by Stickle (1973) is the dry weight of the component (× 100) divided by the entire snail weight including the shell and expressed as grams per 100 gram animal.

Chemical analyses

Individual body components were homogenized in diethyl-ether with a Potter-Elvehjem tissue grinder. The homogenate was centrifuged and the ether-lipid solution was poured into a pretared weighing pan. The tissue pellet was washed with another volume of diethyl-ether, centrifuged and the supernatant was added to the same pan. The pan was reweighed after evaporation of the diethyl ether and the weight of the residue was recorded as lipid.

The tissue pellet was rehomogenized in distilled water to a final volume of ten milliliters. Protein and polysaccharide levels were determined on aliquots of this homogenate.

Polysaccharide was isolated from an aliquot of the homogenate by the method of Barnes, Finlayson and Piatigorsky (1963). Polysaccharide level was determined by the Seifter (1950) modification of the anthrone method. Rabbit liver Type III glycogen was used as a standard.

A one milliliter aliquot of the homogenate was precipitated with ten milliliters of 10% trichloroacetic acid (TCA) and centrifuged. The tissue pellet was then washed with five milliliters of 5% TCA, centrifuged, washed with five milliliters of 5% TCA and recentrifuged. Protein nitrogen in the washed precipitate was determined by standard micro-Kjeldahl techniques which included nesslerization. Protein was determined by multiplying protein nitrogen by 6.25.

Statistical analyses

Each parameter was analyzed as the mean plus and minus the confidence interval at the ninety-five percent level of significance.

RESULTS

Visceral mass levels

Male and female visceral mass protein, lipid, and polysaccharide levels are given in Table I. The protein level of both sexes declined sharply during the 1968–69 egg laying period which lasted from January through March. Protein level was higher in December, 1969 than December, 1968. Lipid level decreased from a November prespawning high to the low point in the annual cycle in Feb-

TABLE I

Biochemical levels of visceral mass in mg dry weight^{-1}.

Month	Males						Females					
	Protein	N	Lipid	N	Poly.	N	Protein	N	Lipid	N	Poly.	N
Sept. 68	384 ± 255	12	165 ± 23	13	81 ± 14	9	500 ± 83	9	141 ± 20	11	59 ± 14	10
Oct. 68	432 ± 39	9	98 ± 12	11	92 ± 16	9	434 ± 28	17	97 ± 6	16	99 ± 15	9
Nov. 68	456 ± 53	9	154 ± 20	9	75 ± 11	8	526 ± 50	10	143 ± 24	10	72 ± 9	10
Dec. 68	444 ± 27	9	95 ± 12	12	67 ± 12	12	514 ± 214	12	112 ± 14	12	52 ± 13	12
Jan. 69	450 ± 40	12	64 ± 11	12	58 ± 12	11	554 ± 91	10	93 ± 11	12	51 ± 6	9
Feb. 69	362 ± 31	12	62 ± 15	12	28 ± 7	12	434 ± 74	11	99 ± 21	12	24 ± 9	12
Mar. 69	305 ± 37	12	86 ± 23	12	65 ± 15	8	395 ± 33	12	80 ± 18	12	56 ± 20	8
Apr. 69	362 ± 78	8	48 ± 13	8	39 ± 11	8	482 ± 83	8	60 ± 21	8	37 ± 11	8
May 69	513 ± 110	6	61 ± 7	8	29 ± 10	8	571 ± 72	8	74 ± 13	8	28 ± 8	7
June 69	401 ± 60	12	76 ± 20	12	57 ± 11	10	436 ± 62	11	73 ± 17	12	46 ± 9	10
July 69	475 ± 37	10	67 ± 14	10	61 ± 19	9	474 ± 46	10	67 ± 10	10	53 ± 17	10
Aug. 69	522 ± 40	7	54 ± 12	8	61 ± 8	8	453 ± 100	8	74 ± 17	8	49 ± 8	8
Sept. 69	487 ± 32	8	141 ± 37	8	83 ± 6	7	587 ± 22	8	125 ± 23	8	75 ± 11	8
Dec. 69	613 ± 34	8	88 ± 31	8	91 ± 17	8	627 ± 57	7	126 ± 23	8	73 ± 15	7

ruary. Male lipid level increased in March, which may have been due to resumed feeding activity or the sharp concomitant decrease in protein level. Males tend to leave the breeding aggregation and begin feeding before females. Female visceral mass lipid level continued to decline through April. Lipid level remained low through the summer months for both sexes and increased sharply from August to September, 1969. Polysaccharide level of both sexes declined continuously from

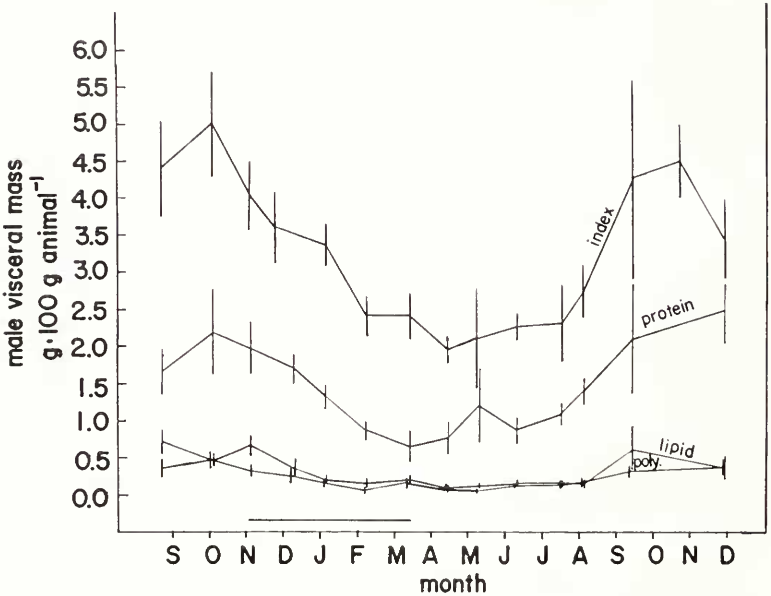

FIGURE 1. Male visceral mass content of the index, protein, lipid and polysaccharide are represented by lines. Vertical lines through each line on the respective sampling dates represent the ninety-five per cent confidence interval about that mean value. The horizontal line at the bottom of the figure indicates the period of male aggregation.

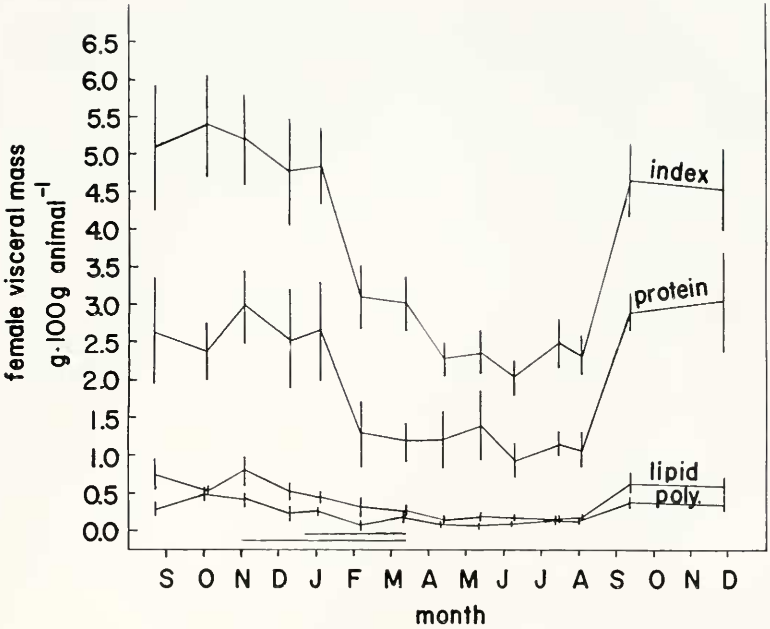

FIGURE 2. Female visceral mass content of the index, protein, lipid and polysaccharide are represented by lines. Vertical lines through each line on the respective sampling dates represent the ninety-five per cent confidence interval about that mean value. The longer horizontal line at the bottom of the figure indicates the period of aggregation and the shorter line represents the period of capsule deposition.

October to February. The sharp increase in polysaccharide level of both sexes during March was caused by a concomitant sharp drop in the protein level. Polysaccharide level reached a second low in May and then climbed consistently until the fall of 1969.

Visceral mass content

Male visceral mass indexes and protein, lipid and polysaccharide contents are given in Figure 1 and female data are given in Figure 2. Protein was the dominant biochemical class and its content closely paralleled seasonal changes in the visceral mass indexes. Lipid content increased just prior to aggregation and spawning and then declined during spawning and the summer months. It increased again during the fall months. Polysaccharide content changed less than protein or lipid but followed the same general pattern as lipid content.

Complex component level and content

Seasonal changes in male testis-digestive gland, remaining visceral mass and foot protein, lipid and polysaccharide level and content are given in Table II. Highest protein levels occurred during the fall in the testis-digestive gland and foot components and the lowest level occurred during the latter part of the aggregation period of February. Protein level in the remaining visceral mass was lowest during September concomitant with a sharp rise in the polysaccharide level. Lipid was much more concentrated in the testis-digestive gland than in the other two components with the maximum level occurring during the fall prior to aggregation and copulation. Polysaccharide level was highest in the remaining visceral mass during the fall and in the foot in September, 1969. The lowest levels in the remaining visceral mass and foot occurred during February and May. The testis-digestive gland polysaccharide level was lower than was found in the other two components throughout the year.

Seasonal changes in component content of protein, lipid, and polysaccharide were predominantly determined by changes in the respective indexes. All three biochemical classes exhibited a distinct seasonal cycle in the testis-digestive gland and remaining visceral mass of being highest in the fall, declining during the winter and spring, remaining stable during the summer and increasing again in the fall. No seasonal cycle of body indexes existed for the foot. The foot was a poor depot for lipid and polysaccharide. Foot protein content was higher in the fall of 1969 than in the same period of 1968.

Seasonal changes in female ovary-digestive gland, capsule-albumin gland, remaining visceral mass and foot biochemical levels and contents are given in Table III. Protein level was highest in the capsule-albumin gland complex. Protein reached the lowest level in the ovary-digestive gland, remaining visceral mass and foot during February but the lowest level was not reached in the capsule-albumin gland until May. This may have been due to the fact that capsule deposition was not completed until the end of March. Protein level was higher in all components in the fall of 1969 than in November, 1968. Lipid was considerably more concentrated in the ovary-digestive gland than in the other components and exhibited a distinct seasonal cycle of being highest before aggregation and lowest during spawning (February) and in May. Polysaccharide was most concentrated in the remaining visceral mass where it exhibited a strong seasonal cycle of being highest in the fall and declining during the winter and spring. Polysaccharide level rose sharply between May and September in the capsule-albumin gland, remaining visceral mass and foot.

Seasonal changes in nutrient content were predominantly due to changes in indexes. Protein content was highest in the ovary-digestive gland where it exhibited a strong seasonal cycle. Capsule-albumin gland protein content increased sharply from September to December while the content of the ovary-digestive gland and remaining visceral mass decreased during the same period. Lipid content was only substantial in the ovary-digestive gland with the other three components being very minor lipid depots. Ovary-digestive gland lipid content exhibited a definite seasonal cycle. Polysaccharide content was higher in the ovary-digestive gland and remaining visceral mass than in the capsule-albumin gland and foot. This was mainly due to differences in the index magnitude. A seasonal cycle was observed in all but the foot.

Biochemical budget for a female snail during capsule deposition

Because female snails do not feed while aggregated it was possible to partition the loss of biomass, protein, lipid and polysaccharide from the visceral mass into

TABLE II

Biochemical composition of male T. lamellosa. *Complex components expressed as level = mg/g dry wt; content = g/100 g animal.*

Component	Month	Index*	Protein			Lipid			Polysaccharide		
			Level	Content	N	Level	Content	N	Level	Content	N
Testis-digestive gland	Nov. 68	2.46	393 ± 45	0.881 ± 0.344	5	233 ± 45	0.584 ± 0.222	6	36 ± 23	0.083 ± 0.063	5
	Feb. 69	0.99	351 ± 74	0.356 ± 0.267	8	142 ± 29	0.145 ± 0.112	8	37 ± 25	0.030 ± 0.022	7
	May 69	0.75	474 ± 75	0.388 ± 0.192	7	93 ± 15	0.068 ± 0.026	8	32 ± 9	0.026 ± 0.015	8
	Sept. 69	2.50	510 ± 52	1.297 ± 0.536	8	219 ± 58	0.558 ± 0.295	8	49 ± 7	0.122 ± 0.044	8
	Dec. 69	1.76	487 ± 73	0.988 ± 0.281	8	151 ± 50	0.322 ± 0.144	8	67 ± 31	0.128 ± 0.040	8
Remaining visceral mass	Nov. 68	1.85	499 ± 93	0.814 ± 0.197	5	38 ± 10	0.067 ± 0.017	6	136 ± 56	0.237 ± 0.100	5
	Feb. 69	1.45	530 ± 70	0.721 ± 0.244	7	25 ± 3	0.035 ± 0.011	8	37 ± 24	0.058 ± 0.048	7
	May 69	1.42	526 ± 125	0.758 ± 0.283	7	34 ± 5	0.047 ± 0.004	8	27 ± 12	0.038 ± 0.018	8
	Sept. 69	1.77	475 ± 44	0.832 ± 0.139	8	33 ± 6	0.058 ± 0.014	8	125 ± 14	0.205 ± 0.041	7
	Dec. 69	1.77	545 ± 58	1.057 ± 0.189	8	22 ± 6	0.043 ± 0.016	8	98 ± 18	0.195 ± 0.059	8
Foot	Nov. 68	0.56	461 ± 63	0.268 ± 0.044	9	36 ± 4	0.021 ± 0.003	9	50 ± 17	0.028 ± 0.010	8
	Feb. 69	0.54	406 ± 57	0.241 ± 0.053	10	27 ± 3	0.015 ± 0.002	12	21 ± 3	0.012 ± 0.003	12
	May 69	0.51	482 ± 81	0.251 ± 0.060	7	31 ± 9	0.016 ± 0.005	8	25 ± 8	0.012 ± 0.004	8
	Sept. 69	0.51	593 ± 101	0.324 ± 0.061	8	24 ± 9	0.013 ± 0.005	8	144 ± 22	0.078 ± 0.013	8
	Dec. 69	0.54	641 ± 93	0.375 ± 0.047	8	17 ± 6	0.010 ± 0.003	6	63 ± 14	0.037 ± 0.009	8

* From Stickle, 1973.

TABLE III

Biochemical composition of female T. lamellosa. *Complex components expressed as level = mg/g dry wt; content = g/100 g animal.*

Component	Month	Index*	Protein			Lipid			Polysaccharide		
			Level	Content	N	Level	Content	N	Level	Content	N
Ovary-digestive gland	Nov. 68	2.91	529 ± 78	1.620 ± 0.531	8	236 ± 43	0.723 ± 0.404	8	37 ± 12	0.121 ± 0.067	8
	Feb. 69	1.11	480 ± 128	0.530 ± 0.220	8	194 ± 62	0.253 ± 0.144	8	25 ± 7	0.028 ± 0.014	8
	May 69	0.81	542 ± 62	0.405 ± 0.114	8	149 ± 33	0.116 ± 0.062	8	27 ± 6	0.021 ± 0.008	8
	Sept. 69	2.47	573 ± 15	1.518 ± 0.205	8	206 ± 36	0.559 ± 0.141	8	39 ± 9	0.106 ± 0.028	8
	Dec. 69	2.05	556 ± 62	1.183 ± 0.263	8	250 ± 51	0.518 ± 0.088	8	48 ± 7	0.102 ± 0.023	8
Capsule-albumin gland	Nov. 68	0.94	601 ± 98	0.596 ± 0.182	8	37 ± 7	0.036 ± 0.010	8	56 ± 18	0.054 ± 0.020	8
	Feb. 69	0.54	687 ± 235	0.450 ± 0.369	8	60 ± 23	0.027 ± 0.008	8	51 ± 24	0.024 ± 0.010	8
	May 69	0.39	552 ± 185	0.222 ± 0.185	8	79 ± 27	0.022 ± 0.006	8	49 ± 14	0.014 ± 0.006	7
	Sept. 69	0.61	768 ± 126	0.441 ± 0.132	8	24 ± 6	0.041 ± 0.010	8	131 ± 45	0.072 ± 0.021	8
	Dec. 69	1.04	841 ± 165	1.021 ± 0.245	7	25 ± 6	0.037 ± 0.008	8	56 ± 13	0.066 ± 0.009	7
Remaining visceral mass	Nov. 68	1.63	484 ± 70	0.823 ± 0.172	8	37 ± 9	0.062 ± 0.014	8	107 ± 19	0.188 ± 0.063	8
	Feb. 69	1.12	450 ± 38	0.516 ± 0.121	7	32 ± 8	0.037 ± 0.010	6	17 ± 8	0.021 ± 0.013	7
	May 69	1.31	580 ± 85	0.768 ± 0.208	8	23 ± 4	0.030 ± 0.009	8	22 ± 10	0.031 ± 0.020	8
	Sept. 69	1.66	557 ± 82	0.952 ± 0.169	8	40 ± 30	0.022 ± 0.005	8	115 ± 24	0.192 ± 0.031	8
	Dec. 69	1.44	577 ± 69	0.865 ± 0.166	8	31 ± 8	0.033 ± 0.009	8	120 ± 29	0.179 ± 0.048	8
Foot	Nov. 68	0.63	501 ± 63	0.334 ± 0.055	9	34 ± 4	0.022 ± 0.002	10	46 ± 12	0.031 ± 0.009	9
	Feb. 69	0.59	402 ± 51	0.241 ± 0.053	10	35 ± 5	0.021 ± 0.003	12	24 ± 6	0.015 ± 0.005	8
	May 69	0.59	581 ± 84	0.386 ± 0.066	8	21 ± 7	0.014 ± 0.005	8	28 ± 7	0.018 ± 0.005	8
	Sept. 69	0.66	589 ± 84	0.365 ± 0.063	8	20 ± 3	0.013 ± 0.002	8	103 ± 32	0.062 ± 0.016	7
	Dec. 69	0.60	622 ± 114	0.372 ± 0.071	8	22 ± 8	0.013 ± 0.003	8	67 ± 18	0.040 ± 0.008	8

* From Stickle, 1973.

Table IV

Biochemical budget for a female snail during aggregation.

Biochem. class	Mg deposited per capsule	Capsules* deposited per female	Mg deposited per female	Mg lost during spawning per female**	Per cent lost as spawn per female	Per cent catabolized per female
Protein	2.3	36.2	83.3	166.1	50	50
Lipid	0.6	36.2	21.7	21.3	102	—
Poly.	0.1	36.2	3.6	9.1	40	60

* From Spight (1972).
** From Stickle (1973).

the production of egg capsules or the catabolic process of respiration. Calculations were based on the average female studied which weighed 11.3208 grams, and was 40.9 mm long (Stickle, 1973). Of the 207 milligrams of biomass lost per female during aggregation 168 milligrams, 81% of the total, were used for the production of egg capsules and 39 milligrams, 19% of the total, were used for female catabolism (Stickle, 1973). Forty-three empty egg capsules were collected from Turn Island after juveniles emerged from them, dried and weighed. The average dry weight was 2.08 ± 0.18 milligrams. Production of the empty capsules accounted for 75.3 milligrams, 20.8 mg per capsule × 36.2 capsules per female, or 36% of the total amount of biomass lost per female. Ninety-two milligrams or 45% of the amount lost per female during aggregation were utilized in the production of embryos and nutritive fluids.

Table IV gives the results of the partitioning of female visceral mass protein, lipid and polysaccharide content. Protein loss accounted for 80% of the biomass lost during aggregation as compared to a loss of 10% due to lipid depletion and 4% due to polysaccharide depletion. These values resulted in a protein:lipid: polysaccharide ultilization ratio of 18.3:2.3:1.0.

The biochemical composition of 78 freshly laid egg capsules with an average dry weight of 4.6 milligrams was: protein—508; lipid—129; polysaccharide—23 and ash—128 milligrams per gram dry weight. The content of each constituent deposited per capsule was the product of the constitutent level and 4.6 milligrams per capsule. The content per capsule was multiplied by 36.2 to give the quantity of each constituent deposited in capsules per female.

Protein utilization by females during aggregation was split evenly between catabolism and production of egg capsules. Slightly more lipid was deposited in egg capsules than was lost from the female visceral mass during aggregation. Forty percent of the polysaccharide lost from the visceral mass was deposited in capsules and 60% was catabolized.

Discussion

Seasonal changes in the biochemical content of all components, except the foot, were predominantly due to changes in indexes and not biochemical level. Many investigators have overlooked this fact when studying seasonal changes in the biochemical composition of molluscs. Giese (1969) has emphasized that molluscs lack discrete nutrient storage depots such as the vertebrate liver, the subdermal and omental adipose tissue of mammals and the fat bodies of lower vertebrates. Therefore nutrient storage occurs primarily through the production of new cellular elements. Seasonal shifts in protein, lipid and polysaccharide levels are merely reflections of their relative rates of synthesis and degradation and are often meaningless with respect to seasonal shifts in their content.

Protein content within the visceral mass was much higher than lipid and polysaccharide content and it exhibited a distinct seasonal cycle. Lambert and Dehnel (1974) also found protein to be the dominant constituent of the gonad and digestive gland in *T. lamellosa.* Giese (1969) reported protein to be the dominant organic constituent in molluscs. The female capsule-albumin gland had the highest protein level but the highest content was found in the ovary-digestive gland. Protein level cycled in all three components of the male. Testis-digestive gland and remaining visceral mass content exhibited a distinct seasonal cycle.

Protein level for comparable tissue was somewhat lower in this study than was reported in Lambert and Dehnel's (1974) work. Part of the difference in the results of the two studies may have been due to methods used. Giese (1966) pointed out that protein determinations based on the Kjeldahl method yield lower values than those obtained from the Lowry method used by Lambert and Dehnel. Population differences also exist. A population of snails from near Juneau, Alaska had much lower protein and polysaccharide levels and higher lipid levels in the visceral mass on all sampling dates than existed in the Turn Island population.

Lipid content was highly concentrated in the gonad-digestive gland complex and its seasonal cycle was mainly due to index changes. Giese (1969) suggests that a lipid value of 5% of dry weight (= 50 mg/g) is a good estimate of structural lipid. Lipid levels exceed 5% in the gonad-digestive gland complex only so that none of the other components acts as a depot area. Lambert and Dehnel (1974) found the lipid level of both the digestive gland and the gonad to be high enough that these components should be considered depots. Transfer of lipid between the two components is unlikely because the level and content of both components followed similar trends throughout the study. Giese (1969) indicates that an inverse relationship between these components provides indirect evidence that nutrient transfer is occurring.

It should be emphasized that the diethyl-ether method used in the present investigation would give lower values than the chloroform-methanol methods utilized by Giese (1969) and Lambert and Dehnel (1974). Structural phospholipids are not soluble in diethyl ether.

Polysaccharide levels and contents were lower than lipid values for most of the study. They were higher in the remaining visceral mass of both sexes than in the other components. Values obtained in this study for the gonad-digestive gland complex agree with those obtained by Lambert and Dehnel (1974) for the gonad and digestive gland analyzed separately. Polysaccharide was likely glycogen because Emerson (1965) found only glucose in the polysaccharide fraction of whole *T. lamellosa.*

Lambert and Dehnel (1974) found glycogen and protein levels of the digestive gland to increase in parallel with the digestive gland index between April and

August. In August the lipid level began to rise, reaching its maximum level in December while glycogen and protein levels fell. Williams (1970) also found changes in total carbohydrate to occur slightly prior to changes in lipid level. Lambert and Dehnel (1974) felt that lipid must have been synthesized from glycogen. They also stated that the correlation between maximum feeding and peak glycogen levels strongly suggests that glycogen is not stored to any great extent but is either metabolized or converted into lipid or protein. The tremendous increase in visceral mass index between August and September, 1969 was explained by Stickle (1973) as being due to the availability of optimal size barnacles for predation by *T. lamellosa*. Polysaccharide level and content increased tremendously between May and September in the male remaining visceral mass and foot. Foot polysaccharide content declined from September to December. A similar large increase in polysaccharide level and content occurred between May and September in the female capsule-albumin gland, remaining visceral mass and foot. Polysaccharide level and content did not change between September and December in any female body component. Lipid content decreased in the male visceral mass (testis-digestive gland and remaining visceral mass). Protein content increased 2.3 fold in the female capsule-albumin gland complex. If seasonal changes in biochemical composition are based on content, polysaccharide does not act as a temporary storage pool from which lipid and protein are synthesized in *T. lamellosa*.

Stickle and Duerr (1970) and Stickle (1971) found *T. lamellosa* to utilize whatever substrate was available at the time of starvation. Lipid was present in female *T. lamellosa* during aggregation. As indicated above, however, it did not appear to be used as a source of energy for the female during aggregation. Might it be destined for use in reproductive activity in a manner similar to the function of galactogen in the pulmonate *Helix pomatia?* May (1932a, b) found galactogen to be present exclusively in the albumin glands and in the eggs, and glycogen exclusively in the rest of the body. When starved *H. pomatia* utilized glycogen reserves for the first ten days before galactogen reserves were drawn upon. Martin (1961) suggested that galactogen acts as a reserve which is not easily drawn upon and enhances the chances of reproductive success.

The foot was a minor depot for protein, lipid and polysaccharide in *T. lamellosa*. Lambert and Dehnel (1974) came to the same conclusion with their study of *T. lamellosa*. Webber (1970) speculated that the foot of *H. cracherodii* may act as a storage depot for metabolic demands of gonad growth. The foot is a predominate body component of *H. cracherodii* but only a minor one in *T. lamellosa* (Stickle, 1973). Giese (1969) stated that the molluscan foot can hardly be considered a lipid storage organ.

Much of the protein deposited in egg capsules was likely used for capsule wall production. Fretter and Graham (1962) summarized the capsule wall composition of *Nucella* (= *Thais*) *lapillus* as being composed of three layers of protein and a little mucoprotein.

Lipid was present in much higher concentration in *T. lamellosa* capsules (12.9%) than has been found in pulmonate and opisthobranch spawn. Bayne (1968) histochemically analyzed the reproductive products of eight gastropods (six pulmonates, one opisthobranch, and one prosobranch). Lipid was present in the nutritive fluid of *Nucella* (= *Thais*) *lapillus* only. Polysaccharide appears to be the nutritive substrate deposited for an energy source of embryonic pulmonate snails (Bayne, 1966; 1968). Stickle (unpublished data) has analyzed the reproductive products of five prosobranch species and five species of opisthobranchs. Lipid levels are much higher in the prosobranch reproductive material (7–17% of dry weight) than in that of opisthobranchs (1–2% of dry weight). This trend holds even when lipid level is placed on a per gram ash free dry weight basis because of the high ash levels in the opisthobranch reproductive material analyzed (35–62% of dry weight). Polysaccharide levels were low for all species of prosobranchs and opisthobranchs studied (1–2% of dry weight) except for the freshwater prosobranch *Viviparus subpurpureus* (9% of dry weight). Protein levels were a reflection of the type of capsular material deposited around the embryos.

Basic metabolic differences exist in the strategies employed by prosobranchs, pulmonates and opisthobranchs to provide nourishment for embryonic development. Phylogenetic, life history and environmental modifications of the biochemical composition of gastropod reproductive products have received little attention by investigators. The advantage of using species which produce encapsulated spawn is that it allows one the opportunity to determine output per female and determine partitioning of biochemical compounds by the female into those going into spawn production and those used for female catabolic activity.

Those gastropods which aggregate and starve while producing egg capsules utilize energy for body maintenance in addition to producing reproductive products. The catabolic expenditure by females during aggregation must be accounted for when determining the efficiency of alternative reproductive strategies. Stickle and Mrozek (1973) found 30% of the prespawning soft body weight of *Fusitriton oregonensis* to be lost during aggregation. Calculations from data presented by Stickle (1973) indicate 34% of the soft body weight of *T. lamellosa* was lost during aggregation.

While there are no data available on the percent of soft body weight lost during spawning by broadcast fertilizing gastropods, data exist for the clam *Tellina tenuis*. Ansell and Trevallion (1967) found the body weight of a standard size clam to drop from 35 to 30 milligrams during spawning which represents a 14% decline in body weight.

Additional information is needed on the percentage of soft parts utilized in the reproductive effort of animals using different reproductive strategies. The present study indicates that the energetic costs of aggregation, starvation and production of encapsulated embryos are just as high as those for the broadcast fertilization reproductive strategy.

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SUMMARY

1. Seasonal changes in protein, lipid and polysaccharide level and content were studied in several body components of *Thais lamellosa*. Male soft body compo-

nents consisted of the visceral mass, including the testis-digestive gland and remaining visceral mass, and the foot. Female soft body components consisted of the visceral mass, including the ovary-digestive gland, capsule-albumin gland, and remaining visceral mass, and the foot.

2. Seasonal changes in protein, lipid and polysaccharide content in body components, except the foot, were predominantly due to changes in indexes and not biochemical level. The foot was not important as a depot for any of the biochemical constituents. Protein was the dominant constituent in the visceral mass, lipid was intermediate in level and content and polysaccharide level and content were lowest.

3. The gonad-digestive gland complex was a lipid depot for both sexes. No other body component of either sex served as a lipid depot.

4. The ovary-digestive gland lipid content was at its maximum value in September but the capsule-albumin gland protein content did not reach its maximum value until December when it was 2.3 times the September value. The accessory reproductive tract reaches its maximum size just prior to capsule deposition.

5. The ratio of protein:lipid:polysaccharide content lost from the female visceral mass during aggregation was 18.3:2.3:1.0. Protein loss was split evenly between female catabolism and egg capsule production. Lipid loss went entirely to egg capsule production. Polysaccharide loss was split between female catabolism and egg capsule production.

6. Individuals interested in the efficiency of alternate reproductive strategies must consider the costs of aggregation and capsule wall deposition to species utilizing this type of strategy. Energetic costs of aggregation, starvation and production of encapsulated embryos are just as high as costs involved in broadcast fertilization among molluscs.

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